BIRDS FROM THE BLUFF DOWNS LOCAL FAUNA, ALLINGHAM FORMATION, QUEENSLAND.

WALTER E. BOLES & BRIAN MACKNESS

A small number of bird fossils have previously been recorded from the early Pliocene freshwater, fluviatile and lacustrine deposits of the Allingham Formation, northwest of Charters Towers, northeastern Queensland. There has been several significant avifaunal discoveries made during recent excavations of the site, most of these being waterbirds. The number of taxa now recognised has almost trebled from previous published accounts and includes at least seven orders, ten families and 15 species-level taxa. A new subspecies of the Purple swamphen, *Porphyrio porphyrio nujagura* subsp. nov., is described. The earliest occurrences of the genera *Anhinga*, *Ardea*, *Cereopsis* and *Progura* in the Australian avifaunal fossil record are also reported. The potential role that the study of fossil birds can play in palaeoecological reconstructions is discussed.

Walter E. Boles, Division of Vertebrate Zoology, Australian Museum, 6–8 College Street, Sydney. Brian Mackness, School of Biological Sciences, University of New South Wales, P.O. Box 1, Kensington New South Wales 2033. Manuscript received 31 July 1993.

Birds have long been considered to be of secondary importance in the examination of fossil assemblages, with the paucity of their occurrence in the fossil record being cited as just one of the reasons for this cursory treatment (Olson 1985). The Australian fossil avifaunal record stretches back to the Cretaceous (Vickers-Rich 1991) and, although there has been a considerable increase in the investigation of fossil birds in recent years, most Tertiary studies have been taxonomic in nature, usually focussing on a single group (e.g. Miller 1963, 1966; Rich 1979; van Tets 1974). The interpretation of palaeoenvironments using fauna has relied almost exclusively on mammals, and indeed the 'Local Fauna' concept (Tedford, 1970) has this as its foundation.

In recent years, however, with an increasing number of palaeoornithologists working in Australia, birds are being used more and more both as biostratigraphic markers (Rich 1979) and as palaeoecological indictors (Boles 1993; Baird 1993).

A variety of taxa has been recovered from the early Pliocene freshwater fluviatile and lacustrine deposits of the Allingham Formation, northwest of Charters Towers, northeastern Queensland (Archer 1976, Bartholomai 1978, Archer & Dawson 1982, Archer 1982, Rich & van Tets 1982). Collectively this assemblage has been called the Bluff Downs Local Fauna (Archer 1976). The only bird mentioned in the original description of the fauna was *Xenorhynchus* [=*Ephippiorhynchus*] *asiaticus* (Archer 1976). Subsequently Rich & van Tets (1982) cited five taxa: *Xenorhynchus* cf. *X. asiaticus*, *Threskiornis* sp., cf. *Dendrocygna* sp., *Numenius* sp. and Charadriiformes. Rich *et al.* (1991) also listed five taxa: *Xenorhynchus* [=*Ephippiorhynchus*] *asiaticus*, *Threskiornis* sp., *Cygnus* sp., *Dendrocygna* sp. and *Numenius* sp. None of these listings offered further elaboration.

MATERIALS AND METHODS

Measurements were taken with vernier calipers accurate to 0.05 mm and rounded to the nearest 0.1 mm. Terminology of bones is primarily from Baumel (1979). Where comparisons were made with published measurements, the methods of measuring followed those adopted in the comparative study; otherwise these largely followed those illustrated by Steadman (1980). Specimens are currently held at the Queensland Museum. All the fossil material examined and all modern specimens used for comparisons were considered to be adults, based on the absence of a '. . . pitted surface of the bone and incomplete ossification of the articular facets' (Campbell 1979: 17).
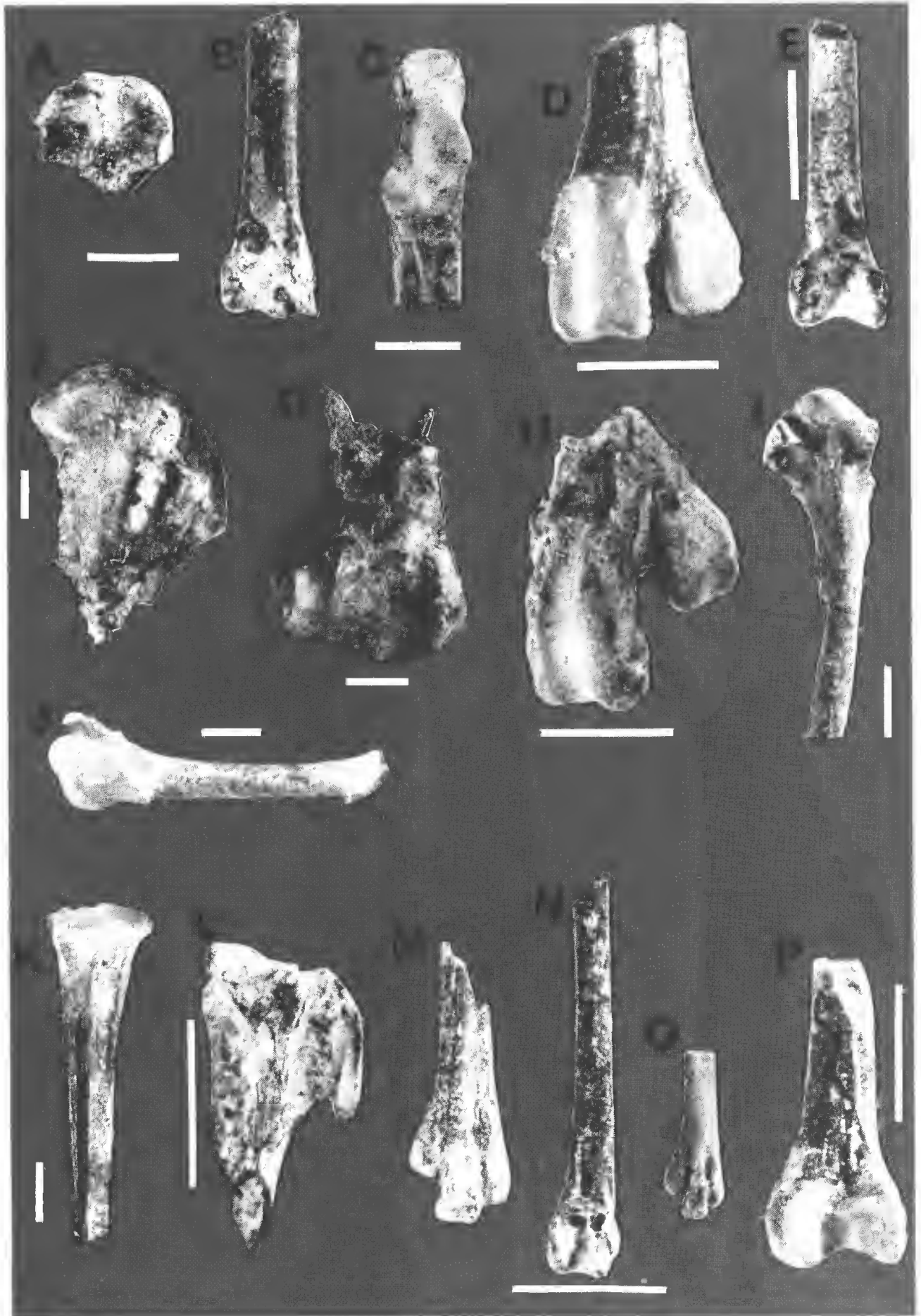
PHALACROCORACIDAE

Phalacrocorax sulcirostris
(Fig. 1a,b)

Material

Proximal right humerus (QM F23242), distal right humerus (QM F23241), possibly from the same bone. Measurements: proximal width 16.8 mm, distal width 11.7 mm, depth of *condylus dorsalis* 7.9 mm. Locality: EVS Site.

Characters

The two fragments are considered to belong to the same species, and possibly the same individual, on the basis of size and configuration. The proximal end is referred to the Phalacrocoracidae on the basis of the reduced *crista pectoralis*, very broad *impressio m. coracorbrachialis* and broad, deep *sulcus ligamentosus transversus*. The distal fragment has a deeply excised *fossa m. brachialis*, which among extant Australian species occurs in *P. sulcirostris* and *P. varius* (Siegel-Causey 1988). The fossil agrees in size with *P. sulcirostris* (proximal width 16.2–17.2 mm, distal width 11.4–13.1 mm, depth of *condylus dorsalis* 7.9–8.6 mm), and is smaller than *P. varius* (proximal width 19.1–21.8 mm, distal width 13.1–14.1 mm, depth of *condylus dorsalis* 9.1 – 9.8 mm).

Remarks

The Little Black Cormorant is widespread in wetlands, prefering open water greater than one metre deep, including large lakes, areas with flooded or fringing trees, and swamps with permanent or semi-permanent water (Marchant & Higgins 1990).

ANHINGIDAE

Anhinga sp.

Material

Proximal right humerus (QM F23653); right carpometacarpus (QM F25776). This material represents a new species and is being described (B. M.) elsewhere. Locality: QM F23653, EVS Site; QM F25776, Main Site.

Remarks

Darters prefer smooth, open water at least 0.5 m deep, including permanent waterbodies, large lakes with shallow vegetated edges and semi-permanent swamps (Marchant & Higgins 1990).

ARDEIDAE

cf. *Ardea picata*
(Fig. 1e)

Material

Distal right tibiotarsus (QM F23243). Measurements: distal width 7.7 mm, depth of *condylus lateralis* 7.4 mm, depth of *condylus medialis* 7.9 mm. Locality: EVS Site.

Characters

The fossil is smaller and relatively more gracile than *Egretta novaehollandiae*, *E. garzetta*, *A. intermedia*, *Ixobrychus flavicollis* and *Nycticorax caledonicus*, but a good match in size and robustness for *Ardea picata* (distal width 6.3–8.0 mm, depth of *condylus lateralis* 6.5–7.6 mm, depth of *condylus medialis* 6.6–7.9 mm). It is not possible to assign the distal tibiotarsus to any particular genus of herons on morphological features. Payne & Risley (1976) found no consistent differences in the tibiotarsi within this family.

◄ FIGURE 1. Avian fossils from the Bluff Downs Local Fauna. Bars equal 10 mm. Bars are shared by **A** and **B**, and by **M,N** and **O**. Queensland Museum registration numbers are given in parentheses.
A. *Phalacrocorax sulcirostris*, proximal right humerus (F 23242): **B**. *Phalacrocorax sulcirostris*, distal right humerus (F 23241); **C.** *Threskiornis* sp. cf. *T. molucca*, cranial right coracoid (F 23257); **D**. *Threskiornis* sp. cf. *T. molucca*, distal right tarsometatarsus (F 23256); **E**. *Ardea* sp. cf. *A. picata*, distal right tibiotarsus (F 23243); **F**. *Ephippiorhynchus asiaticus*, proximal left humerus (F 23244); **G**. *Ephippiorhynchus asiaticus*, distal left humerus (F 23245); **H**. *Phoenicopterus* sp. cf. *P. ruber*, distal right tarsometatarsus (F 23252); **I**. *Dendrocygna arcuata*, proximal right humerus (F 23248); **J**. *Progura* sp. cf. *P. naracoortensis*, carpometacarpus (F 23258); **K**. *Progura* sp. cf. *P. naracoortensis*, proximal left tarsometatarsus (F 23259); **L**. *Porphyrio porphyrio nujagura* subsp. nov., proximal right tarsometatarsus (F 23250); **M**. Rallidae gen. and sp. indet. 2, distal left tarsometatarsus (F 23255); **N**. Rallidae gen. and sp. indet. 1, distal left tibiotarsus (F 23254); **O**. *Porzana* sp., distal left tarsometatarsus (F 23253); **P**. cf. *Numenius* sp., distal right femur (F 23251).

Remarks

Virtually all herons are associated with water, the type of wetland preferred and the manner in which it is utilised depending on the species. The Pied Heron occurs in shallow wetlands, including floodplains and swamps (Marchant & Higgins 1990).

CICONIIDAE

Ephippiorhynchus asiaticus
(Fig. 1f,g)

Material

Proximal left humerus (QM F23244); distal left humerus (QM F23245). Measurements: proximal width 44.8 mm, distal width 34.4 mm, depth of *condylus dorsalis* 18.7 mm. A '. . . fragment of tarsometatarsus (QM F7036)' cited by Archer (1976: 385) was not examined. Locality: QM F23244 AB Site; QM F7036, QM F23245 Main Site.

Characters

The proximal fragment agrees with the Ciconiidae and differs from the Gruidae, the only other similar taxon, by having *caput humeri* proportionally shorter, *intumescentia* less inflated and *fossa pneumotricipitalis* larger. The distal fragment resembles the former family, but not the latter, by having *tuberculum supracondylare ventrale* narrow and ridge-like, and *processus supracondylaris dorsalis* prominently produced.

Remarks

The Black-Necked Stork, Australia's only extant member of this family, inhabits mainly open water up to 0.5 m deep, including extensive sheets over grassland, shallow swamps and pools on floodplains (Marchant & Higgins 1990).

THRESKIORNITHIDAE

Threskiornis sp. cf. *T. molucca*
(Fig. 1 c,d)

Material

Cranial right coracoid (QM F23257); distal right tarsometatarsus missing *trochlea metatarsi IV* (QM F23256). Measurements: coracoid, cranial end of *processus acrocoracoideus* to caudal end of *cotyla scapularis* 20.6 mm, depth of *processus acrocoracoideus* 9.4 mm; tarsometatarsus, depth of *trochlea metatarsi III*

c. 8.0 mm, dorsal length of *trochlea metatarsi III* 8.2 mm. Locality: QM F23256 EVS Site; QM F23257 Main Site.

Characters

The tarsometatarsus is assigned to *Threskiornis* rather than *Platalea* because *trochlea metatarsi II* agrees with the former in being less recessed plantarly relative to *trochlea metatarsi III* (in medial view). It agrees in size with *molucca* (depth of *trochlea metatarsi III* 8.4 mm, plantar length of *trochlea metatarsi III* 8.0 mm), which is larger than *spinicollis* (depth of *trochlea metatarsi III* 7.3–7.4 mm, plantar length of *trochlea metatarsi III* 7.1–7.3 mm).

Allocation of the coracoid to *Threskiornis* rather than *Platalea* is on the basis of having a narrower *processus acrocoracoideus* (in dorsal view), *cotyla scapularis* proportionally further from *processus acrocoracoideus*, and *processus procoracoideus* curving less mediad.

Living *T. spinicollis* and *T. molucca* are not separable on measurements that can be taken on the fossil coracoid (cranial end of *processus acrocoracoideus* to *cotyla scapularis*: *spinicollis* 20.4–21.8 mm, *molucca* 20.2–22.8 mm; depth of *processus acrocoracoideus*: *spinicollis* 11.7–12.1 mm, *molucca* 11.3–12.1 mm). These species differ somewhat in robustness of the shaft; however, damage to the Bluff Downs material precludes comparison. The coracoid is referred to the same taxon as the tarsometatarsus. Because material is limited and the living species are morphologically quite similar, a more definite identification is not made.

Remarks

The Australian White Ibis habitat preferences include shallow water over soft substrates, in swamps and open water, and muddy flats (Marchant & Higgins 1990).

PHOENICOPTERIDAE

Phoenicopterus sp. cf. *P. ruber*
(Fig. 1h)

Material

Partial distal right tarsometatarsus lacking *trochlea metatarsi IV* (QM F23252). Measurements: medial depth of *trochlea metatarsi II* c. 7.9 mm, lateral depth of *trochlea metatarsi II* 8.4 mm, dorsal width of *trochlea metatarsi III* 10.3 mm, lateral depth of *trochlea*

metatarsi III c. 9.1 mm, dorsal width of *trochlea metatarsi III c.* 7.6 mm, plantar length of *trochlea metatarsi III* 11.7 mm. Locality: Main Site.

Characters

This specimen is identified as a flamingo on the basis of the following characters (most from Rich *et al.* 1987): *trochlea metatarsi II* short relative to *trochlea metatarsi III*; distal end of *trochlea metatarsi II* broader than plantar border; *trochlea metatarsi II* twisted plantarly and laterally from front of tarsometatarsus; and *trochlea metatarsi III* narrow and deep. Reference of this fragment to this species is made on the basis of size rather than on diagnostic morphology.

The measurements of the Bluff Downs specimen are a good match for those of extant *P. ruber* given by Rich *et al.* (1987), and the specimen is therefore tentatively assigned to this taxon. This follows the practice of Rich *et al.* (1987: 207), who, faced with limited and undiagnostic material, segregated the forms on size and ' . . . provisionally retained the generic and specific names that have priority as a convenience until more complete material allows a better evaluation of the systematic positions of the Pliocene and Quaternary flamingoes of Australia'.

Remarks

There are few records of flamingoes in Australia away from the centre of the continent. Rich *et al.* 1991 have recorded an undetermined flamingo from the late Miocene Alcoota Local Fauna, northern Australia. Living *P. ruber* of Africa frequents mainly saline or alkaline lakes, estuaries and lagoons, seldom alighting on fresh water (Brown *et al.* 1982). Similar conditions have been proposed for central Australian lake deposits yielding flamingo remains. The Alcoota Locality during the late Miocene is considered by Murray & Megirian (1992: 214) to have represented '. . . a small but permanent, possibly spring-fed pond or lake, sometimes expanding to a temporary, large, shallow lake.'

ANATIDAE

Cygnus atratus

Remarks

This taxon was cited by Vickers-Rich (1991) without further elaboration. This material has not been examined in this study. Locality: Main Site.

Cereopsis sp.

Material

A proximal carpometacarpus fragment (QM F23260). This material, probably representing the extant species *C. novaehollandiae*, will be described (B.M.) elsewhere. Locality: EVS Site.

Remarks

This species inhabits grasslands and terrestrial wetlands, occasionally entering water.

Dendrocygna arcuata
(Fig. 1i)

Material

Proximal right humerus (QM F23248). Measurements: proximal width *c.*18.3 mm, depth of *caput humeri* 6.0 mm. Locality: Main Site.

Characters

The Anserinae and Dendrocygninae are separated from other Anatidae by the combination of prominent capital shaft ridge directed towards the *caput humeri*, attachment for *caput ventrale* of *M. humerotriceps* extending virtually to *caput humeri*, and area of attachment of *M. pectoralis* on the *tuberculum dorsale* is elevated and somewhat circular (Woolfenden 1961). The Anserinae is unrepresented in Australasia except by the aberrant *Cereopsis*, which is diagnosable by several unique characters. The Bluff Downs specimen is an excellent fit for *Dendrocygna*, agreeing in size with *D. arcuata*, the smaller of the two Australian species.

Remarks

The Water Whistling-Duck prefers fresh, deep permanent waters with emergent vegetation (Marchant & Higgins 1990).

Nettapus sp.

Material

An almost complete left carpometacarpus (QM F23249). This material probably represents a new species and will be described (B.M.) elsewhere. Locality: EVS Site.

Remarks

Pygmy-geese are wholly aquatic on terrestrial wetlands, preferably deep (greater than 1m), permanent water bodies, with abundant floating

and submerged vegetation (Marchant & Higgins 1990).

MEGAPODIIDAE

Progura sp. cf. *P. naracoortensis*
(Fig. 1j,k)

Material

Carpometacarpus (QM F23258) lacking *os metacarpale minor*. Proximal left tarsometatarsus (QM F23259) lacking most of the *hypotarsus*. Measurements: carpometacarpus, proximal width (dorsal) 17.5 mm, (ventral) 15.0 mm; tarsometatarsus, proximal width 19.5 mm. Locality: EVS Site.

Characters

A tentative identification has been made on size. Van Tets (1974) published measurements for the two known species: proximal width of tarsometatarsus, *P. naracoortensis* 21–23 mm, *P. gallinacea* 26–29 mm; dorsal and ventral widths of carpometacarpus, *P. gallinacea* 27 x 16 mm; a carpometacarpus of *P. naracoortensis* was not available. The Bluff Downs material is smaller and older than that of either species. Here it is tentatively referred to the smaller *P. naracoortensis*, but it may represent an undescribed species.

The tarsometatarsus of *Progura* is separated from that of extant genera of Australian megapodes by the following combination of characters: hypotarsus situated more laterad, *sulcus hypotarsi* more laterally situated relative to *eminentia intercondylaris*, *cotyla medialis* nearly size of *cotyla lateralis* in cranial view with dorsal border rounded and projecting dorsally about the same extent as *cotyla lateralis*, medial border of *corpus tarsometatarsi* straight (less concave), and *sulcus extensorius* broader and deeper and extending further distad.

The carpometacarpus is distinguished by its combination of *processus extensorius* more proximally directed, proximal border of *facies articularis radiocarpalis* of *trochlea carpalis* rounded (not pointed), caudal border of *facies articularis ulnocarpalis* of *trochlea carpalis* rounded (not flattened) and extended ventrally only slightly more than *facies articularis radiocarpalis*, and *os metacarpale majus* slightly caudally curved.

Remarks

Previous records of *Progura* are from coastal and subcoastal areas of eastern and southeastern Australia. Not enough is known about the ecology of these animals for them to be useful bioecological indicators. Van Tets (1974) hypothesised that, based on relative leg lengths, the longer-legged *P. gallinacea* was a rainforest species, whereas *P. naracoortensis* inhabited open scrub land. Van Tets (1984) later suggested that, because these two species are usually found together, they could represent a single, sexually dimorphic species.

RALLIDAE

Porzana sp.
(Fig. 1o)

Material

Distal left tarsometatarsus (QM F23253). Measurements: distal width 4.3 mm. Locality: EVS Site.

Characters

This specimen is larger than *Porzana tabuensis* (distal width 3.7 mm) or *P. pusilla* (3.3 mm) and about the same size as *P. fluminea* (4.3 mm) and *P. cinereus* (4.7 mm). Compared with these latter two species, *trochlea metatarsi* are thinner and more splayed, *trochlea metatarsi II* appears slightly less directed plantarad, and *incisurae intertrochlearis* are wider. The specimen is abraded on the trochlear surfaces, and some of these differences could be artefacts of this wear. Osteological characters given by Olson (1970) and Steadman (1986) between *P. cinerea* and other species of *Porzana* are not relevant to this partial element.

Remarks

Most rails are associated with water. The smaller species, including most *Porzana*, are usually shy, spending most of their time in dense waterside vegetation. *Porzana cinerea* also requires floating vegetation.

Genus and species indet. 1
(Fig. 1n)

Material

Distal left tibiotarsus (QM F23254). Distal width 5.1 mm, depth of *condylus lateralis c.* 5.3 mm, depth of *condylus medialis c.* 5.3 mm. Locality: EVS Site.

Remarks

The fossil represents a small to medium rail between the sizes of *Porzana cinereus* (distal width 4.2 mm, depth of *condylus lateralis* 3.9 mm, depth of *condylus medialis* 4.1 mm) and *Gallirallus philippensis* (distal width 6.0 mm, depth of *condylus lateralis* 6.0 mm, depth of *condylus medialis* 6.0 mm). There are several extant Australasian genera within this size range with which the specimen should be compared, *Dryolimnas* (*sensu* Olson 1973), *Rallina* and *Rallicula*.

Genus and species indet. 2.
(Fig. 1m)

Material

Distal left tarsometatarsus (QM F23255). Measurements: distal width 7.1 mm, depth of *trochlea metatarsi III* 3.8 mm. Locality: EVS Site.

Characters

This specimen comes from a larger and somewhat more robust species than the previous indeterminate rail. It is similar in size to *Amaurornis olivacea* (distal width 6.7–6.9 mm, depth of *trochlea metatarsi III* 3.2–3.6 mm) and *Gallinula ventralis* (distal width 7.4 mm, depth of *trochlea metatarsi III* 4.3 mm). This fossil is also similar in morphology to *A. olivacea*, and probably could be tentatively referred to that species; however, it seems prudent to await more extensive material and comparisons with a greater range of genera before taking this action.

Porphyrio porphyrio nujagura subsp. nov.
(Fig. 1l)

Material

Proximal right tarsometatarsus (QM F23250). Measurements: proximal width 9.7 mm, proximal depth 11.4 mm, length of *hypotarsus* 10.4 mm, width of *hypotarsus* 5.6 mm. Locality: EVS Site.

Characters

Agrees with *Porphyrio* and differs from other genera of Australian rails, including the genera of larger forms (*Gallinula*, including *Tribonyx*; *Fulica*; *Gallirallus australis*) by having a distally directed projection on the plantodistal end of the *hypotarsus* (in other genera, the *hypotarsus* curves smoothly into the shaft).

There are four Recent species of *Porphyrio* from Australasia: three flightless Australasian species (*mantelli*, New Zealand; *albus*, Lord Howe Island – extinct; and *kukwiedei*, New Caledonia – extinct; Balouet & Olson 1989); and *porphyrio*, the only member of the genus now occurring in Australia. The first three are much larger and robust than *porphyrio*. The Bluff Downs specimen shows no morphological differences from *porphyrio* but is smaller than either sex of this sexually size dimorphic species (Australian *porphyrio*: proximal width 10.7–12.5 mm, proximal depth 12.4–13.7 mm, length of *hypotarsus* 11.0–13.0 mm, width of *hypotarsus* 6.2–6.9 mm). Compared with measurements given by Steadman (1988: Table 2), it is also smaller than most extralimital populations of the *P. porphyrio* superspecies, except *P. porphyrio* from Bechuanaland and *P. poliocephalus* of Thailand.

Etymology

The specific name is from the Gugu-Yalanji dialect word *nujagura*, meaning 'prehistoric times' (Oates *et al.* 1964).

Remarks

The only extant Australian species of comparable size not examined was *Eulabeornis castaneoventris*, a mangrove specialist, for which no skeletons exist. The end of the shaft is jagged, indicating that the break occurred before fossilisation. This individual was probably a victim of a predator or scavenger. The Purple swamphen prefers permanent freshwaters with good cover of rushes and other larger waterplants, at least along the water's edge, usually in the proximity of more open grazing areas (Marchant & Higgins 1993).

SCOLOPACIDAE

cf. *Numenius* sp.
(Fig. 1p)

Material

Distal right femur (QM F23251). Measurements: distal width 10.0 mm, depth of *condylus lateralis* 8.7 mm, depth of *condylus medialis* c. 7.0. Locality: Main Site.

Characters

This specimen appears to represent a large sandpiper. It is substantially larger than all Australasian taxa except for *Numenius*, for which it is also a good match in morphology. Because

the distal femur has limited diagnostic value and the bone is slightly abraded, identification is not attempted beyond cf. *Numenius* sp.

Remarks

Some members of this family are restricted to coastal areas; others occur in freshwater wetlands (Lane 1987). Larger *Numenius* species are coastal, whereas *N. minutus* extends well into subcoastal regions.

DISCUSSION

Taphonomy

All fossils were recovered from a series of massive lacustrine clays from Main Quarry (Archer 1976) and Elaine's Vertebrae Site (Mackness unpublished information). Most of the bones were not complete and showed post-depositional breakage and fragmentation. An exception was the tarsometatarsus of *Porphyrio porphyrio nujagura*, the jagged edge of which suggested predation or scavenging while the body was still relatively fresh. There was little evidence of transportation wear and, even though there was no articulation, it is probable that the birds died in reasonable proximity to the site of deposition. An examination of bone textures suggests that there was little subaerial prediagenetic exposure and that most bones were quickly buried or submerged.

Vickers-Rich (1991) suggested a bias in avifaunal fossil deposits toward medium-sized birds (e.g. ducks, flamingos, burhinids) and larger birds (emus) to the exclusion of smaller birds. Although the bird assemblage recovered to date is consistent with this prediction, large scale wet-screening of sediments presently being undertaken may result in the recovery of smaller birds. The depositional environment obviously favours the preservation of waterbirds: these are also common

Coracoid	■ (1)
Humerus	▬▬▬ (4)
Carpometacarpus	▬▬▬ (4)
Femur	▬ (2)
Tibiotarsus	▬ (2)
Tarsometatarsus	▬▬▬▬ (5)

FIGURE 2. Summary of avian skeletal elements recovered from Bluff Downs Site.

in central Australian Tertiary sites (Vickers-Rich 1991). The proportions of the different bone elements found fossilised at Bluff Downs are summarised in Figure 2. All are regarded to be the most durable elements (Napawongse 1981; Rich & Baird 1986; Vickers-Rich 1991).

Palaeoecology

Archer (1976) has suggested that the Bluff Downs Local Fauna may have been riparian. The large number of non-avian fossils recovered from the Bluff Downs site include both terrestrial and aquatic forms, with neither predominating. The mammals provide no definitive indication of what the terrestrial environment may have been like, although a typically rainforest-dwelling pseudocheirid possum is presently being described (B.M), along with an enigmatic family of marsupials (Mackness *et al.* 1993).

Three types of crocodiles have been recovered, including two large aquatic and one terrestrial form (Willis & Mackness in prep.). Studies of the molluscan fauna have revealed a diverse suite of species, some requiring specific aquatic niches that range from high energy fluvatile environments to stagnant lacustrine regimes (Mackness, unpublished data). It is evident from this faunistic 'mix' that there was a complex series of aquatic environments available either ephemerally or on a permanent basis.

Various authors (Frith 1959, Braithwaite & Frith 1969, Braithwaite 1975, Fjeldså 1985) have suggested a relationship between the distribution of waterbird species and habitat types. Fjeldså (1985) found poor correlation between avian communities and classifications based on vegetation types. Indicator species, e.g. *Porphyrio* and *Phalacrocorax*, are present in several of Fjeldså's classifications. Given the taphonomic evidence of minimal transportation and the nature of the sediments themselves, the Bluff Downs avifauna appears to be a biocoenotic assemblage, which may represent several depositional episodes. While most of the taxa identified, or their closest extant relatives, are relatively nonspecific in their preferences for wetland types, some utilise a range of microhabitats within wetland environments. Living species of *Nettapus* are more strict in their requirements than most, being generally confined to deeper water with considerable floating vegetation.

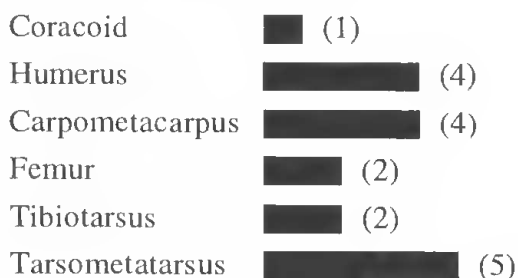Living *Cereopsis novaehollandiae* graze on grasslands, whereas living phoenicopterids are

TABLE 1. Comparison of Australian Pliocene avifaunal assemblages. Data for Chinchilla and Kanunka from Rich *et al.* (1991) and Vickers-Rich (1991).

Family	Bluff Downs	Chinchilla	Kanunka
Casuariidae	–	X	X
Pelecanidae	–	X	X
Phalacrocoracidae	X	X	X
Anhingidae	X	X	X
Ardeidae	X	–	X
Ciconiidae	X	--	X
Threskiornithidae	X	–	–
Phoenicopteridae	X	–	X
Anatidae	X	X	X
Accipitridae	–	–	X
Gruidae	–	–	X
Megapodidae	X	X	–
Rallidae	X	X	–
Otididae	–	–	X
Scolopacidae	X	–	–
'Charadriiformes'	–	X	X

normally found in saline environments today. Disregarding these novelties, the remaining taxa comprise a waterbird community that differs little from that which now occurs in tropical Australia, such as in the wetlands of Kakadu National Park, Northern Territory, an area supporting seasonal floodplains, waterholes, rivers, ephemeral swamps and permanent lakes. From the avian assemblage, it is probable that at least part of Bluff Downs consisted of similar wetlands during the Pliocene.

Comparisons with other Pliocene faunas

Most Pliocene deposits have yielded bird fossils. Many are too fragmentary for identification while others have not yet been studied (Vickers-Rich 1991). Apart from the Bluff Downs Local Fauna, both the Chinchilla and Kanunka Local Faunas have significant avian components (Table 1). All three avifaunas are considered to be wetland assemblages, with the dominant families represented containing mostly wetland specialists. In these, most of the same families are represented. However long-legged wading birds (Ciconiiformes, Phoenicopteriformes) are absent from Chinchilla.

REFERENCES

ARCHER, M. 1976. Bluff Downs local fauna. Pp. 383–396 in Archer, M. & Wade, M., Results of the Ray E. Lemley Expeditions, Part I. The Allingham Formation and a new Pliocene vertebrate fauna from northern Australia. *Memoirs of the Queensland Museum* **17**: 379–397.

ARCHER, M. 1982. Review of the dasyurid (Marsupialia) fossil record, integration of data on phylogenetic interpretation, and suprageneric classification. Pp. 397–443 *in* 'Carnivorous marsupials', ed. by M. Archer. Royal Zoological Society of New South Wales: Sydney, New South Wales.

ARCHER, M. & DAWSON, L. 1982. Revision of

marsupial lions of the genus *Thylacoleo* Gervais (Thylacoleonidae, Marsupialia) and Thylacoleonid evolution in the late Cainozoic. Pp. 477–494 *in* 'Carnivorous marsupials', ed. by M. Archer. Royal Zoological Society of New South Wales: Sydney, New South Wales.

ARCHER, M. & WADE, M. 1976. Results of the Ray E. Lemley Expeditions, Part 1. The Allingham Formation and a new Pliocene vertebrate fauna from northern Australia. *Memoirs of the Queensland Museum* **17**: 379–397.

BALOUET, J. C. & OLSON, S. L. 1989. Fossil birds from Late Quaternary deposits in New Caledonia. *Smithsonian Contributions to Zoology* **469**: 1–38.

BARTHOLOMAI, A. 1978. The Macropodidae (Marsupialia) from the Allingham Formation, Northern Queensland. Results of the Ray E. Lemley Expeditions, Part 2. *Memoirs of the Queensland Museum* **18**: 127–143.

BAIRD, R. F. 1993. Pleistocene avian fossils from Pyramids Cave (M–89), eastern Victoria, Australia. *Alcheringa* **17**: 383–404.

BAUMEL, J. J. 1979. Osteologia. Pp. 53–121 *In* 'Nomina Anatomica Avium', ed. by J. J. Baumel., A. S. King., A. M. Lucas., J. E. Breazile & H. E. Evans. Academic Press: London.

BOLES, W. E. 1993. A logrunner *Orthonyx* (Passeriformes: Orthonychidae) from the Miocene of Riversleigh, northwestern Queensland. *The Emu* **93**: 44–49.

BRAITHWAITE, L. W. 1975. Managing waterfowl in Australia. *Proceedings of the Ecological Society of Australia* **8**: 107–128.

BRAITHWAITE, L. W. & FRITH, H. J. 1969. Waterfowl in an inland swamp in New South Wales. *C.S.I.R.O. Wildlife Research* **14**: 1–16.

BROWN, L. H., URBAN, E. K. & NEWMAN, K. 1982. 'The Birds of Africa'. Vol. 1. Academic Press: London.

CAMPBELL, K. E., Jr. 1979. The non-passerine Pleistocene avifauna of the Talara Tar Seeps, northwestern Peru. *Royal Ontario Museum, Life Sciences Contribution* **118**: 1–203.

FJELDSÅ, J. 1985. Classification of waterbird communities in south-eastern Australia. *The Emu* **85**(3): 141–9.

FRITH, H. J. 1959. The ecology of wild ducks in inland New South Wales. I. waterfowl habitats. *C.S.I.R.O. Wildlife Research* **4**: 97–107.

LANE, B. A. 1987. 'Shorebirds in Australia'. Nelson: Australia.

MACKNESS, B. S., ARCHER, M., & MUIRHEAD, J. 1993. An enigmatic family of marsupials from the early Pliocene Bluff Downs Local Fauna of northeastern Queensland. Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics. April 19–21 Adelaide. (Abstract)

MARCHANT, S. & HIGGINS, P. J. (Coordinators). 1990. 'Handbook of the Birds of Australia, New Zealand and Antarctica' Vol. 1. Oxford University Press: Melbourne.

MARCHANT, S. & HIGGINS, P. J. (Coordinators). 1993. 'Handbook of the Birds of Australia, New Zealand and Antarctica' Vol. 2. Oxford University Press: Melbourne.

MEES, G. F. 1982. Birds from the lowlands of southern New Guinea (Meraukc and Kocmbe). *Zoologische Verhandelingen* **191**: 1–188.

MILLER, A. H. 1963. The fossil flamingoes of Australia. *The Condor* **65**: 289–299.

MILLER, A. H. 1966. The fossil pelicans of Australia. *Memoirs of the Queensland Museum* **14**: 181–190.

MURRAY, P. F. & MEGIRIAN, D. 1992. Continuity and contrast in middle and late Miocene vertebrate communities from the Northern Territory. *The Beagle* **9**: 195–218.

NAPAWONGSE, P. 1981. A taphonomic study of bird bone degredation in a fluviatile environment. BSc (Hons) thesis. Monash University, Clayton.

OATES, W., OATES, L., HERSHBERGER, H., HERSHBERGER, R., SAYERS, B, & GODFREY, M. 1964. 'Gugu-Yalangi and Wik-Munkan language studies'. Occasional Papers in Aboriginal Studies. **2**: 1–146. Australian Institute of Aboriginal Studies.

OLSON, S. L. 1970. The relationships of *Porzana flaviventer. The Auk* **87**: 805–808.

OLSON, S. L. 1973. A classification of the Rallidae. *Wilson Bulletin* **85**: 381–416.

OLSON, S. L. 1985. The fossil record of birds. Pp. 79–252 in 'Avian Biology' Volume 8, ed. by D. S. Farner., J. R. King & K. C. Parkes. Academic Press: London.

PAYNE, R. B. & RISLEY, C. J. 1976. Systematics and evolutionary relationships among the herons (Ardeidae). *Miscellaneous Publications of the Museum of Zoology, University of Michigan* **150**: 1–115.

PRINGLE, J. D. 1987. 'The Shorebirds of Australia'. Angus & Robertson: Sydney.

RICH, P. V. 1979. The Dromornithidae, a family of large, extinct ground birds endemic to Australia. *Bureau of Mineral Resources Bulletin* **184**: 1–196.

RICH, P. V. & BAIRD, R. F. 1986. History of the Australian avifauna. *Current Ornithology* **4**: 97–139.

RICH, P. V. & VAN TETS, G. F. 1982. Fossil birds of Australia and New Guinea: their biogeographic, phylogenetic and biostratigraphic input. Pp. 235–384 *in* 'The Fossil Vertebrate Record of Australasia'. ed. P. V. Rich & E. M. Thompson. Monash University Offset Printing Unit: Clayton.

RICH, P. V., VAN TETS, G. F., RICH, T. H. & MCEVEY, A. R. 1987. The Pliocene and Quaternary flamingoes of Australia. *Memoirs of the Queensland Museum* **25**: 207–225.

RICH, T. H., ARCHER, M., HAND, S. J., GODTHELP, H., MUIRHEAD, J., PLEDGE, N. S., FLANNERY, T. F., WOODBURNE, M. O., CASE, J. A., TEDFORD, R. H., TURNBULL, W. D., LUNDELIUS, E. L. Jr., RICH, L. S. V., WHITELAW, M. J., KEMP, A. & RICH, P. V. 1991. Australian Mesozoic and Tertiary terrestrial mammal localities. Pp. 1005–1058 in 'Vertebrate Palaeontology of Australasia', ed. by P. Vickers-Rich, J. Monaghan, R. F. Baird & T. H. Rich. Pioneer Design Studio: Melbourne.

SIEGEL-CAUSEY, D. 1988. Phylogeny of the Phalacrocoracidae. *The Condor* **90:** 885–905.

STEADMAN, D. W. 1980. A review of the osteology and paleontology of turkeys (Aves: Meleagridinae). *Contributions in Science, Natural History Museum of Los Angeles County* **330:** 131–207.

STEADMAN, D. W. 1986. Two new species of rails (Aves: Rallidae) from Mangaia, southern Cook Islands. *Pacific Science* **40:** 27–43.

STEADMAN, D. W. 1988. A new species of *Porphyrio* (Aves: Rallidae) from archeological sites in the Marquesas Islands. *Proceedings of the Biological Society of Washington* **101:** 162–170.

TEDFORD, R. H. 1970. Principles and practices of mammalian geochronology in North America. Pp. 666–703 in 'Proceedings of the North American Paleontological Convention', ed. by E. L. Yochelson. Allen Press: Lawrence, Kansas.

VAN TETS, G. F. 1974. A revision of the fossil Megapodiidae (Aves), including a description of a new species of *Progura* De Vis. *Transactions of the Royal Society of South Australia* **98:** 213–224.

VAN TETS, G. F. 1984. A checklist of extinct fossil Australasian birds. Pp. 469–475 in 'Vertebrate Zoogeography & Evolution in Australasia', ed. by M. Archer & G. Clayton. Hesperian Press: Carlisle.

VICKERS-RICH, P. 1991. The Mesozoic and Tertiary history of birds on the Australian plate. Pp 722–808 in 'Vertebrate Palaeontology of Australasia'. ed. by P. Vickers-Rich, J. M. Monaghan, R. F. Baird & T. H. Rich. Pioneer Design Studio: Melbourne.

WOOLFENDEN, G. E. 1961. Postcranial osteology of the waterfowl. *Bulletin of the Florida State Museum* **6:** 1–129.